ART. XL. — *Development of the Brachiopoda.* Part I. Introduction; by CHARLES E. BEECHER, Ph.D. (With Plate XVII.)

THE Brachiopoda have been so carefully studied, that any new general conclusions regarding them must naturally be based upon features not heretofore considered. In other classes of animals, such important results have recently been reached by the application of the law of morphogenesis as defined by Hyatt, that the writer was led to study the Brachiopoda from this standpoint. The facts observed by this method are mainly new to the class, and considerably affect the taxonomic positions and affinities of the various families and genera.

The value of the stages of growth and decline in work relating to phylogeny and classification is now generally admitted. The memoirs of Hyatt, Jackson, and others, amply show that the clearest and simplest understanding of a group may thus be reached. The application of the principles of growth, acceleration of development, and mechanical genesis, form the main factors in the studies here made. The geologic sequence of genera and species in this connection is also of the greatest importance, for in this way the development of ancient species may be studied, which in their adult condition represent nealogic or nepionic stages of later forms.

The prolific development of the Brachiopoda, both in point of numbers and variety of genera and species, together with their geological history, mark this group as one which should furnish important data for the study of its genesis and of the limits of a specialized variation in a single class. Moreover, as its culmination was reached in paleozoic time, the group should afford illustration of many principles of evolution.

The main characters common to the class of Brachiopoda are as follows: the bivalve shell; the pedicled or fixed condition; the animal composed of two pallial membranes intimately related to the shell; a visceral sac; and two arms or appendages near the mouth. The extreme range of variation does not eliminate any of these features, and, consequently, no univalve or multivalve forms are found, nor any strictly free swimming species, nor growths or modifications adapting the organism to a pelagic life. Thus, the limits of modification are narrowly restricted as compared with those of several other classes, i. e. the Echinodermata and the Pelecypoda, but the thousands of known species of Brachiopoda show what differentiation has taken place within these limits.

The Protegulum.

The first important observation to be noted is, that all brachiopods, so far as studied by the writer, have a common form of embryonic shell, which may be termed the *protegulum*.* The protegulum is semicircular or semielliptical in outline, with a straight or arcuate hinge line, and no hinge area. A slight posterior gaping is produced by the pedicle valve being usually more convex than the brachial. The modifications noted are apparently due to accelerated growth, by which characters primarily nealogic become so advanced in the development of the individual as to be impressed finally upon the embryonic shell. This feature is well shown in the development of Orbiculoidea and Discinisca, and is reserved for discussion under these genera.

As the protegulum has been observed in about forty genera† representing nearly all the leading families of the class, its general presence may be safely assumed. In size it varies in different genera and species. The range is from ·05 to ·60^{mm}. A similar range in the prodissoconch of pelecypods has been noticed by Dr. Robert T. Jackson. The protoconch of cephalopods and gastropods also varies greatly. In all these classes, the size of the initial shell has no special relation to the mature form, and it seems to have little significance in related genera or species.

The structure of the protegulum has been described as corneous and imperforate. In all probability it is the same for the entire class, whether among the corneous and phosphatic linguloids and discinoids, or the terebratuloids and other forms having carbonate of calcium shells. Professor E. S. Morse, in describing the early stages of Terebratulina,‡ says: "A heart-shaped corneous shell is formed even at this early stage, for in several cases I met with it where the softer portions had been removed by Paramæcia." Similarly, in the genus Cistella according to Kowalevski:§ "En même temps la coquille se forme, par suite du dépôt sur la cuticule chitineuse des minces couches de calcaire, dans lesquelles on ne voit point encore les perforations tubulaire." Previous to this stage,

* From πρώ, early, and τέγος, a covering.

† Atretia (Cryptopora), Chonetes, Cistella, Conotreta, Crania, Craniella, Discina, Discinisca, Glottidia, Gwynia, Kraussina (Megerlina), Laqueus, Leptæna, Lingula, Lingulops, Linnarssonia, Liothyrina, Magellania (Macandrevia), Martinia, Muhlfeldtia, Obolus? Œhlertella, Orbiculoidea, Orthis group, Pholidops, Productella, Rhynchonella (Hemithyris), Schizambon, Schizobolus, Schizocrania, Schizotreta, Spirifer, Streptorhynchus (Orthotetes), Stropheodonta, Strophomena, Terebratella, Terebratulina, Thecidium (Lacazella), Trematis, Tropidoleptus, Zygospira.

‡ Embryology of Terebratulina. Mem. Boston Soc. Nat. Hist., vol. ii, p. 257, vide figures 68, 76, pl. viii. 1873.

§ Developpement des Brachiopodes, Kowalevski. Analyse par MM. Œhlert et Deniker, pp. 65, 67. 1883.

"Les lobes du manteau commencent alors à se recouvrir d'une cuticule épaisse et rigide que ne leur permet plus de se mouvoir que dans le sens vertical."

From the minuteness and the tenuous nature of the protegulum, its fossil preservation in an unaltered condition would not be anticipated. Neither would it be found on the beaks of mature shells, whether recent or fossil. In rare cases of unusually perfect conservation of the beaks, the protegulum is retained, but frequently its form and characters are exhibited after its removal, by the impression left in the surrounding calcareous test. To study the features of the protegulum, and the early stages in the growth of the shell, it is very desirable and often necessary to have young and well-preserved specimens. The rapid encroachment of the pedicle on the ventral beak commonly obliterates, at an early period, all traces of the protegulum and early nepionic stages. While in the brachial valve, abrasion from foreign objects, or against the deltidial covering, or the pedicle itself, usually removes all early lines of growth or nepionic characters. In general, fully matured shells, recent or fossil, do not furnish material for a study of the incipient growth stages.

Affinities.—In looking for a prototype preserving throughout its development the main features of the protegulum, and showing no separate or distinct stages of growth, the early primordial form hitherto known as Kutorgina, Billings, is at once suggested. This genus, as shown below, includes two distinct types, for one of which the name Paterina is proposed.*

* The strict definition of Kutorgina limits it to calcareous shells, such as are found near Swanton, Vermont, often occurring as casts in the limestone. The original description of *Obolella cingulata* by Billings (Geology of Vermont, vol. ii, p. 948, figs. 347–349, 1861) seems to include two species. One, represented by figures 347 and 349 (loc. cit.), agrees with phosphatic species having a straight hinge line as long as the width of the shell. The other, shown in figure 348, has a calcareous test, shorter hinge, flattened brachial valve, and convex pedicle valve with arching beak. Upon the latter species, the genus was founded, and it has been recognized as the type by C. D. Walcott (Bulletin U. S. Geol Surv., No. 30, p. 102, pl. ix, figs. 1, 1*a*, *b*, 1886.) The species represented by Billings in figures 347 and 349 resembles *Obolus labradoricus* (fig. 345, loc. cit.), and is represented by Walcott (l. c , pl. ix, figs. 2, 2*a*, *b*) and referred by him also to Kutorgina. Mr. Walcott recognizes two groups of species, which are classified (p. 102) as: "shell structure calcareous (*K. cingulata*, *K. Whitfieldi*) or horny (*K. Labradorica*, *K. sculptilis*)."

An examination of specimens representing both groups, leads the writer to consider *Kutorgina cingulata* and *Obolus labradoricus* of Billings as generically distinct. Therefore the name *Paterina* is here proposed to include species of the type of *Obolus labradoricus.* This name is intended to express the primitive ancestral characters which it possesses, Plate XVII, figures 1, 2. Exfoliated specimens of *Paterina labradorica* show a roughened area on the cast, each side of the median line near the beak. These probably represent muscular attachments. Sections of the shell show no hinge area as described in *K. cingulata.* A study of the latter would doubtless present distinct stages of growth. The

The valves of Paterina are subequal, the pedicle valve being a little more elevated than the brachial. They are semielliptical in outline. In mature specimens, all lines of growth, from the nucleal shell to the margin, are unvaryingly parallel and concentric, terminating abruptly at the cardinal line. In other words, no changes occur in the outlines or proportions of the shell during growth, through the nepionic and nealogic stages up to and including the completed ephebolic condition. The resemblance of this form to the protegulum of other brachiopods is very marked and significant, as it represents a mature type having only the common embryonal features of other genera. It is of further importance as representing, in many species, an early condition of nepionic growth subsequent to the protegulum, during which the proportions and features of the shell undergo no modification except increase in size. This is termed the *paterina stage.* It is well shown in the brachial valve of *Orbiculoidea minuta*, Hall, Plate XVII, figure 5.

Modifications from acceleration.—The modifications in the form of the protegulum are due to the influence of accelerated growth, by which nepionic and sometimes nealogic features are pushed forward, or appear earlier in the history of the individual, so as to become impressed upon the early embryonic shell. Only a brief review of these changes will be noted here, as a fuller description properly belongs under the discussions of the various genera and families. Naturally, the greatest departure from the normal protegulum is exhibited in the most variable and specialized valve, the pedicle valve. The nearly equivalve genera, as Lingula and Glottidia, present almost no modification. In the ventral valve of Linnarssonia and Orbiculoidea (Plate XVII, fig. 7), the protegulum has a hinge more or less arcuate. Discinisca shows a subcircular pedicle protegulum with a pedicle notch, and the evidence of any hinge in the brachial is very slight, Plate XVII, figures 8, 9. The discinoid character appearing in the second and third nepionic stage of the paleozoic Orbiculoidea (Plate XVII, fig. 6), has become so accelerated in neozoic and recent Discinisca as to produce a discinoid protegulum.

The strophomenoid shells usually retain a normal protegulum in the brachial valve, but from the acceleration of the discinoid stage in the pedicle valve, the protegulum has an abbreviated hinge and arcuate hinge line, Plate XVII, figures 13, 14, 15.

dissimilar valves, arcuate ventral beak, and mesial depression, could be developed only by passing through several well-marked phases. This in itself seems sufficient for a separation were no other characters present.

No marked variation has yet been observed among the spire bearing genera, nor has any been seen in the terebratuloids or rhynchonelloids further than the radii on the protegulum of Atretia (Cryptopora). Possibly this feature in Atretia is an inheritance from the radiate character of the shell in the Rhynchonellidæ. It may be, however, one of the features consequent upon its fragile nature and deep sea habitat, as observed among other abyssal shells.

Differences in the Valves.

The dissimilarity in the form and relations of the two valves progressively increases in the following genera: Lingula, Terebratulina, Cistella, Discinisca, Thecidium (Lacazella), and Crania. Lingula is nearly equivalve, both valves bearing a close resemblance to each other. In Terebratulina and Cistella, the two valves are more strongly specialized, while in Discinisca, Thecidium, and Crania, they are quite unlike.

Two important organic characters accompany and partake of a similar amount of variation; (*a*) the length and direction of the pedicle, and (*b*) the position and structure of the pedicle opening. Lingula with a long, fleshy, mobile pedicle receives uniformly disposed axial impacts on the valves, and, therefore, with equal physiological reactions, equality in size and form is produced. Terebratulina and most of the other terebratuloids and rhynchonelloids have a shorter and less flexible pedicle. As a whole the motions of the animal are more restricted; the pedicle opening is confined mainly to one valve; the valves, consequently, are differently related to the environment, and express this difference in their dissimilarity. In these examples, also, the inclination of the pedicle to the longitudinal axis, or of the shell to the surface of support, agrees, *pari passu* with the amount of unlikeness in the valves, except when the pedicle is so shortened as to interfere with their free movement. To this inclination is probably due the difference in the action of the forces from without.

Normally, in Lingula, the pedicle is in direct linear continuation with the axis of the shell. Terebratulina and Magellania are inclined at an angle of 40° to the surface of support, but in Cistella and Muhlfeldtia, this is increased to about 70°. In the latter genera, although the position of the axis is nearly vertical, the shortening of the pedicle precludes more than a slight elevation and rotation of the organism. The more the pedicle opening is confined to one valve the greater is the difference between both.

Passing to Discinisca, the pedicle is found to be at right angles to the longitudinal axis, and the valves become strictly an upper and a lower. The lower rests upon the

object of support, and the animal is capable of raising and rotating it only to a slight degree. Under such circumstances, the lower valve is wholly different in its relations to the environment, and, naturally, it expresses the greatest dissimilarity in the two valves of any genus yet discussed. In some allied genera, as Discina (type *D. striata*) and Schizotreta, where the pedicle is small and the lower valve rises above the object of support, a similar form in both valves is again produced by the conical growth of the lower valve.

More primitive types, as Acrotreta and Acrothele, having the plane of the brachial valve at right angles to the direction of the pedicle, retain a marginal upper beak, while the lower is elevated, subcentral, and perforate. These features in Acrotreta and Discina resemble, in a measure, those in the rudistes. In Acrotreta as in Caprotina, the upper valve shows its normal affinities, while the other has become highly modified and dissimilar. But in Discina and Hippurites, the hinge line is lost, and the apex of the upper valve is subcentral. This conical habit of growth in erect attached organisms has been explained as the physiological reaction from equal radial exposure to the environment. It constitutes the law of radial symmetry, ably discussed by Haeckel, Jackson, Korshelt, and Heider. Its application to the Brachiopoda can be made mainly in forms having the pedicle perforation subcentrally located in the lower valve.

In Thecidium and Crania, the calcareous union of the lower valve to the object of support represents the extreme of unlike conditioning, and such forms exhibit the greatest difference in the features of the opposite valves. Crania being probably derived from discinoid stock is without proper hinge. In the history of its development, so far as known, it does not show beyond the protegulum, an early hinged condition. Hence there is no indication of direct derivation from hinged forms. A false hinge is sometimes present, but it clearly shows a secondary mechanical adaptation, and not a phylogenetic character. On the other hand, true hinged attached genera, such as Thecidium (Lacazella), Davidsonia, and Strophalosia, possess this feature as a later ancestral character, and, in their chronological history, tend to shorten and gradually eliminate it. An illustration of this is seen in the succession of the species in Strophalosia, or in the ontogeny of one of the Permian species. *Strophalosia Goldfussi*, in early nealogic stages, has a hinge line about equal to the width of the shell, but in mature individuals, it is usually less than one-half the width. This reduction of the hinge and ostrean form of growth are in accordance with the deductions and observations made upon the Oyster and its allies by Jackson, and the mechanical principles are evidently the same in both cases.

One of the most conspicuous examples of a difference in the form of the valves is shown in the abnormal genus Proboscidella. In early nealogic stages, it resembles an ordinary Productus. Afterwards, probably from burrowing in the mud, the ventral valve becomes extravagantly developed anteriorly into a calcareous tube. This is accomplished by the excessive growth of the anterior and lateral margins. Then an infolding takes place until the lateral edges unite, after which the tube is built up by concentric increment around the free end. The resemblance of Proboscidella to Aspergillum is quite marked, except that, in the latter genus, the tube is formed from the growth and union of two valves instead of one.

From the morphological differences of the pedicle and brachial valves, it will be seen that the highest modifications occur in the former; while the variations in the latter are expressed mainly as adaptive reactions or accommodations to these changes. The explanation of the fact that greater alteration takes place in the pedicle valve evidently lies not in the greater plasticity of this member, but in its more highly specialized and differentiated external form, and mainly in its being the lower and attached valve.

No account is taken here of the crura, loops, and spires of the brachial valve, so characteristic and important in many families and genera. These are evidently processes developed by the internal requirements of the animal and are not affected by the environment. Therefore, they are internal calcified organs independent of the form or manner of growth of the external covering. This is shown by the fact, that, in each group, there is a frequent recurrence of similar general external features, whether in crurate, looped, or spire bearing genera.

Genesis of Form.

The principal characters shared by the two valves are the general outline and the hinge. In typical and generalized forms, as Lingula, Terebratulina, Cistella, and Discinisca, considered as before in regard to length of pedicle, freedom of movement, and direction of longitudinal axis to the object of support, we find a key to these types of structure. In the individual development of Terebratulina, as shown by Morse, we first have the early embryonic shell (protegulum), with a short pedicle and straight hinge. The next stage retains both these characters, but the valves have become more unequal and the pedicle opening confined to the fissure of one valve. The result is a shell very much like Argiope or Megerlia (Megathyris and Muhlfeldtia), to which

Professor Morse also called attention. The same author next showed that the succeeding stage had a comparatively long pedicle, and a shell linguloid in form. Afterwards, the defining of the pedicle opening, shortening of the pedicle and truncation of the ventral beak, produced the final characteristic external features of Terebratulina. The deduction from this example and from Lingula is, that genera having pedicles sufficiently long to admit of freedom of axial movement have elongate and rostrate shells. The shortening of the pedicle brings the posterior part of the shell in more or less close proximity to the object of support, and, as growth cannot take place in that direction, it increases laterally, resulting in broader forms with extended hinge areas, as in many species of Cistella, Scenidium, Muhlfeldtia, Terebratella, Kraussina, etc.

The variety known as *Muhlfeldtia truncata*, var. *monstruosa*, Davidson, further shows how discinoid characters may be produced in an entirely different type of shell. A specimen was found by the writer in a position which readily gave the solution to its variation from the normal species. It was attached to a foreign object under the hinge line of a large mature specimen of *M. truncata*, thus forcing the axis and plane of the valves into parallelism with the object of support. In this way, the pedicle emerged at right angles to the axis. The growth of the shell and the increase in the size of the pedicle caused the latter to encroach on the substance of the lower beak, forming a dorsal perforation or pedicle-notch, which in this example amounted to an arc of 180°. As the ventral valve was the upper and the dorsal the lower, with the pedicle opening through the latter, only the abnormal position of the shell can account for this anomalous discinoid condition. In the development of Orbiculoidea, a true discinoid genus, it will be seen that during the early stages it had a straight hinge and marginal beaks, Plate XVII, figures 5, 6, 7. Then, from its procumbent position and peripheral growth, the pedicle became more and more enclosed by the lower valve, until in Schizotreta (fig. 11) and Acrothele (fig. 12), the opening finally became subcentral.

The resemblance between this form of growth and habit and Anomia is very suggestive. Morse and Jackson have shown, that from an early normal, bivalve, hinged shell, the right valve, in its subsequent growth surrounds the byssus, which occupies much the same position and performs a function similar to the pedicle of Discinisca and Orbiculoidea. Peripheral growth also causes the initial shell to recede from the margin. Another instance is thus furnished of a discinoid habit in an organism otherwise entirely different. It is there-

fore evident, that the discinoid form is purely due to the mechanical conditions of growth. Hence the writer believes, that any bivalve shell with the plane parallel to the object of support, and attached by a more or less flexible, very short organ, as a byssus or a pedicle, without calcareous cementation, assumes a discinoid mode of growth.

The conditions of radial symmetry and ostrean growth were briefly mentioned in a preceding section, and need only be cited here as resulting from the cemented state of fixation, as shown in species of Thecidium, Strophalosia, and Crania.

A long pedicle accompanies elongate shells with short hinges. A short pedicle causes extended hinge growth when the plane of the valves is ascending or vertical, but a discinoid form results when the plane of the valves is horizontal.

Types of pedicle openings.

M. Deslongchamps is one of the few writers who have given much consideration to the characters of the pedicle opening. His studies, although mostly confined to the terebratuloids and later spire bearing genera, conclusively show the importance of this feature.* In a recent paper by the writer,† attention was called to the persistence and embryonic features of this portion of the shell. "It has been shown by J. M. Clarke and the writer, that all species, so far as examined, possessing a true deltidium in the adult state, show that it was gradually developed in early stages of growth, by concrescence along the lateral margins of an open triangular area. Also, that all species furnished with a pedicle-sheath have it fully developed in the earliest growth-stages which have been observed for these species, and the subsequent growth of the individual does not materially alter its general characters, except that it is sometimes retrogressive, the parts becoming atrophied or functionally obsolete. A feature of such importance, and so intimately connected with the embryonal growth of the shell, must be given considerable significance in discussing the various genera in which it is present or absent." At that time, the development and true interpretation of these different features of the pedicle opening and the early stages of the shell had not been studied sufficiently, and a more general application of the principles involved could not then be made. The results of later studies give prominence to these characters, and show that they furnish a method for an ordinal grouping of the genera of brachiopods. This is found to agree with the chronological

* Note sur le développement du deltidium chez les brachiopodes articulés. Bull. Soc. Géol. France. 2e Ser. T. XIX, pp. 409–413, pl. IX, 1862.

† This Journal, vol. xl., p. 217, Sept. 1890.

history of the class, as well as with the anatomical and shell characters, and therefore it is believed to be a natural and reliable subdivision.

The first and simplest type of pedicle opening is in shells with a posterior gaping of the valves, through which the pedicle protrudes in line with the axis. It is shared more or less by both valves, although, generally, the greater portion of the periphery is included by the pedicle valve. The genera Paterina and Lingula afford types of this form of pedicle opening.

The second type is characterized by a pedicle wholly confined to the lower valve, and emerging at right angles to the plane of the valves. In primary forms, it is not entirely surrounded by shell growth, but occupies a sinus, slit, or fissure. A further specialization carries it quite within the periphery, and it finally becomes subcentral. A serial illustration of this type is presented in the genera Schizocrania, Orbiculoidea, Discinisca, Schizotreta and Acrothele. The group probably terminates with forms like Crania and Pholidops, as shown by the development of the brachial valve and from internal characters. The development of the lower valve, however, has not been observed as yet in either of these genera.

The third form is an accelerated derivative of the second. During the first nepionic stage of shell growth, the pedicle is enclosed by the substance of the ventral valve. The perforation remains submarginal, and does not tend to become centralized as in the preceding group. The initial pedicle opening may be maintained by further growth, forming a pseudodeltidium; or it may be merged into the hinge opening by resorption of the shell or by pedicle abrasion. Orthisina, Leptæna, Strophomena, Chonetes, and Stropheodonta furnish illustrations of the first condition, and the second is represented in Tropidoleptus and in the groups of Orthis.

The fourth type in its incipient stage marks a return to the simple conditions of the first, but in early nepionic stages the pedicle is confined to the ventral beak, and deltidial plates are developed in the majority of species. These plates at maturity may entirely limit the pedicle opening below, so that the pedicle emerges immediately under the beak, or encroaches upon the substance of the beak itself. This type of opening is shown by Zygospira, Spirifer, Rhynchonella, Terebratulina, Magelliana, etc.

The only divisions of the class which have had continued existence are the Arthropomata and Lyopomata, proposed by Owen in 1858.* Subsequently, various authors gave names to

* Encycl. Brit., 8th ed., vol. xv, p. 301, 1858.

express other characters, but all included the same elements in the two divisions. Professor Huxley's terms, the Articulata and Inarticulata, have also come into current use, and are convenient to express the nature of the union of the valves. All the names proposed for these divisions by Owen, Bronn, Huxley, Gill, and King, are based upon (1) the intestinal canal whether ending in an anus or in a blind sac, (2) the relative proportions of the viscera and brachia to the shell cavity, and (3) the character of the union of the valves.

If, as Agassiz has said,* orders should be founded upon facts of development or embryology, the ordinal division into groups expressing the genesis of an important common character should furnish a satisfactory classification. The Articulata and Inarticulata do not appear to have a primary developmental basis in nature. These names may be conveniently retained as two divisions or sub-classes, but they fail to express the true relationships of the various groups included in them.

In 1883, Dr. Waagen (Palæontologia Indica) proposed a classification comprising six suborders, founded partly on the pedicle opening and on the form of the brachial supports. Two of his groups, the Mesokaulia and Aphaneropegmata, are nearly equivalent in extent to the Atremata and Protremata now proposed. Daikaulia and Gasteropegmata of Waagen are here included in the Neotremata, and the Telotremata comprise the Kampylopegmata and Helicopegmata of the same author. With the transfer of some genera in his suborders, they may properly be recognized and serve further to differentiate the class into comprehensive groups.

After this preliminary discussion, the four groups proposed can be defined and understood. The special details with full illustration and demonstration of the development and affinities in each group are left for future consideration. At present it is aimed to give only the general results which have been reached through the study of individual development (ontogeny) among various species representing the families of nearly the entire class. Of the sixteen families of Brachiopoda recognized by Œhlert in Fischer's "Manuel de Conchyliologie," fifteen have thus been studied and determined. The genera marked by an asterisk have been examined somewhat in detail. The others have been investigated partly from adult specimens, and from the published descriptions of the genera.

* Methods of Study in Natural History, L. Agassiz. 8th ed., p. 76, 1873.

Atremata.

(α, priv., and $\tau\rho\tilde{\eta}\mu\alpha$, perforation.)

Plate xvii, figures 1–4.

Protegulum semicircular or semielliptical; hinge line straight or slightly arcuate. Growth taking place mainly around the anterior and lateral margins, never enclosing or surrounding the pedicle, which in all stages emerges freely between the two valves, the opening being more or less shared by both. Valves inarticulate.

Including the genera:

Dignomia.	*Leptobolus.	Obolus.
Dinobolus.	*Lingula	*Paterina.
Elkania.	Lingulasma.	Paterula.
Glossina.	*Lingulops.	Rhynobolus.
*Glottidia.	Monomerella.	Trimerella.
Lakhmina.	Obolella.	

Neotremata.

($\nu\varepsilon\acute{o}\varsigma$, young, and $\tau\rho\tilde{\eta}\mu\alpha$, perforation.)

Plate xvii, figures 5–12.

Protegulum as in the preceding order in primitive forms, becoming more circular, and with shorter and more arcuate hinge in the pedicle valve of derived types. Growth of the brachial valve tending to become peripheral. In the opposite valve, the pedicle more or less surrounded by progressive nealogic growth posterior to the initial hinge. Pedicle fissure remaining open in primitive mature forms, becoming enclosed in secondary forms during nealogic stages, and in derived types enclosed in early nealogic or nepionic stages. Valves inarticulate.

Including the genera:—

Ancistocrania.	*Discinopsis.	*Orbiculoidea.
Acrothele.	Helmersenia.	Pseudocrania.
Acrotreta.	Iphidea.	*Rœmerella.
*Conotreta.	Kayserlingia.	*Schizambon.
*Crania.	Lindstrœmella.	*Schizobolus.
*Craniella.	*Linnarssonia.	*Schizocrania.
Craniscus.	Mesotreta.	Siphonotreta.
*Discina.	*Œhlertella.	*Trematis.
*Discinisca.		

Protremata.

(πρῴ, early, and τρῆμα, perforation.)

Plate xvii, figures 13–21.

Protegulum of the brachial valve as in the Atremata. In the pedicle valve, it has become modified through acceleration to an elliptical or circular form with arcuate hinge. Pedicle enclosed in early nepionic stages by shell growth; posterior covering (pseudo-deltidium) retained at maturity, or resorbed or abraded in nealogic stages, so that the pedicle protrudes between the two valves. The stages of growth, in general, represent (1) a paterina stage, with straight hinge line and pedicle opening shared by both valves; (2) a discinoid stage, without straight hinge, pedicle enclosed by concentric peripheral growth of pedicle valve; and (3) a straight hinged condition, with pedicle opening either retained or merged into fissure of hinge area. Valves articulate.

Including the genera:—

Amphigenia.	*Lacazella.	Productus.
Aulosteges.	*Leptæna.	*Rhipidomella.
Bactrynium.	Leptænisca.	Schizophoria.
Bilobites.	Lyttonia.	Sieberella.
Camarella (group).	Meekella.	Streptis.
Camarophoria.	Mimulus.	*Streptorhynchus.
*Chonetes.	Oldhamina.	Stricklandinia.
Clitambonites.	*Orthis (group).	Strophalosia.
Conchidium.	Orthisina.	*Stropheodonta.
Davidsonella.	*Orthotetes.	*Strophomena.
Davidsonia.	Pentamerella.	*Strophonella.
Daviesiella.	Platystrophia.	Thecidella.
Derbya.	*Plectambonites.	*Thecidium.
Enteletes.	Porambonites?	Thecidopsis.
Eudesella.	Proboscidella.	Triplecia.
Hemipronites.	*Productella.	*Tropidoleptus.
Hipparionyx.		

Telotremata.

(τέλος, last, and τρῆμα, perforation.)

Plate xvii, figures 22–28.

Protegulum as in Atremata. Pedicle opening shared by both valves in nepionic stages, usually confined to one valve in later stages, and becoming more or less limited by two deltidial plates in ephebolic stages. Arms supported by calcareous crura, spirals, or loops. Valves articulate.

Including the genera:—

Acanthothyris.
Ambocœlia.
Amphiclina.
*Athyris.
*Atretia (Cryptopora).
*Atrypa.
Bifida.
Bouchardia.
Centronella.
*Cistella.
Clorinda.
*Cœlospira.
Cœnothyris.
Cryptonella.
Cyrtia.
Cyrtina.
Dayia.
Dictyothyris.
Dielasma.
Dimerella.
Disculina.
Eatonia.
Eudesia.
Eumetria.
Glassia.
Grunewaldtia.
*Hemithyris.
Hindella.
Ismenia.
Karpinskya.
Kayseria.
Kingena.
Koninckella.
*Koninckina.
*Kraussina.
*Laqueus.
Leptocœlia.
Liorhynchus.
*Liothyrina.
*Macandrevia.
Magas.
*Magellania.
*Martinia.
Martinopsis.
Megathyris.
Megalanteris.
*Megerlina.
Merista.
*Meristella.
*Meristina.
*Muhlfeldtia.
Nucleospira.
Pentagonia.
Peregrinella.
Platydia.
Rensselæria.
Reticularia.
Retzia.
*Rhynchonella.
Rhynchonellina.
Rhynchoporina.
Rhynchotrema.
*Rhynchotreta.
*Spirifer.
Spiriferina.
Spirigerella.
Stringocephalus.
Suessia.
Syringothyris.
*Terebratella.
Terebratula.
*Terebratulina.
Terebratuloidea.
Thecospira.
Trematospira.
Trigonosemus.
Uncinulus.
Uncites.
Zellania.
*Zygospira.

Yale Museum, New Haven, Conn., March, 21, 1891.

EXPLANATION OF PLATE XVII.

Atremata.

FIGURE 1.—Brachial valve of *Paterina labradorica*, Billings. × 3.
FIGURE 2.—Pedicle valve of young specimen. × 3.
Primordial. *Near Georgia, Vermont.*
FIGURE 3.—Apex of pedicle valve of *Glottidia Audebarti*, Brod. × 25.
FIGURE 4.—The same; brachial valve; showing more distinctly terminal protegulum. × 25. Recent. *Beaufort, North Carolina.*

Neotremata.

FIGURE 5.—Upper valve of nepionic *Orbiculoidea minuta*, Hall; representing protegulum (p) and paterina stage. × 25.
FIGURE 6.—More advanced condition; showing acquisition of discinoid characters. × 25.
FIGURE 7.—Lower valve of young specimen; showing protegulum and open pedicle notch. × 25.
Devonian, Marcellus Shale. *Avon, New York.*
FIGURE 8.—Accelerated, discinoid, dorsal protegulum of *Discinisca lævis*, Sowerby, corresponding to nealogic stage of *Orbiculoidea minuta*, figure 6. × 25.

FIGURE 9.—Ventral protegulum of same species similarly modified, agreeing with figure 7. × 25.

FIGURE 10.—Lower valve of same species; showing submarginal position of pedicle opening. Natural size. Recent. *Callao, Peru.*

FIGURE 11.—Lower valve of *Schizotreta tenuilamellata*, Hall; showing centripetal tendency of pedicle opening. Natural size.
Niagara Group. *Hamilton, Ontario.*
(Pal. N. Y. Extract from vol. viii, pl. IVE, fig. 10, 1890.)

FIGURE 12.—Lower valve of *Acrothele subsidua* (after Linnarsson); showing subcentral position of pedicle opening. Natural size.

Protremata.

FIGURE 13.—Dorsal protegulum and early nepionic growth lines of *Plectambonites segmentina*, Angelin. × 80. Upper Silurian. *Gothland, Sweden.*

FIGURE 14.—Dorsal protegulum of *Chonetes scitulus*, Hall. × 80.
Hamilton Group. *Thedford, Ontario.*

FIGURE 15.—Accelerated discinoid ventral protegulum of *Chonetes granuliferus*, Owen; showing pedicle notch. × 80.
Coal Measures. *Manhattan, Kansas.*

FIGURE 16.—Discinoid nepionic stages of ventral valve of *Orthotetes elegans*, Bouch. × 25. Compare with figure 12 of Acrothele.
Devonian. *Ferques, France.*

FIGURE 17.—Nepionic stages of *Stropheodonta perplana*, Conrad; showing pedicle perforation, pseudo-deltidium, and hinge area. × 25.
Hamilton Group. *Falls of the Ohio.*

FIGURE 18.—Ventral nepionic discinoid stage of *Strophomena rhomboidalis*, Wilck. × 25.

FIGURE 19.—Profile of the same. × 25.
Lower Helderberg Group. *Albany County, New York.*

FIGURE 20.—Hinge of a specimen 2^{mm} in length; showing deltidial covering and hinge area.

FIGURE 21.—Ventral view of specimen having same dimensions; showing nepionic and nealogic stages, and relative proportions of pedicle opening and shell at this stage. Niagara Group. *Waldron, Indiana.*
Figures 20 and 21 are taken from "Development of Some Silurian Brachiopoda," Mem. N. Y. State Museum, vol. i, No. 1, pl. II, figs. 2, 12, 1889.

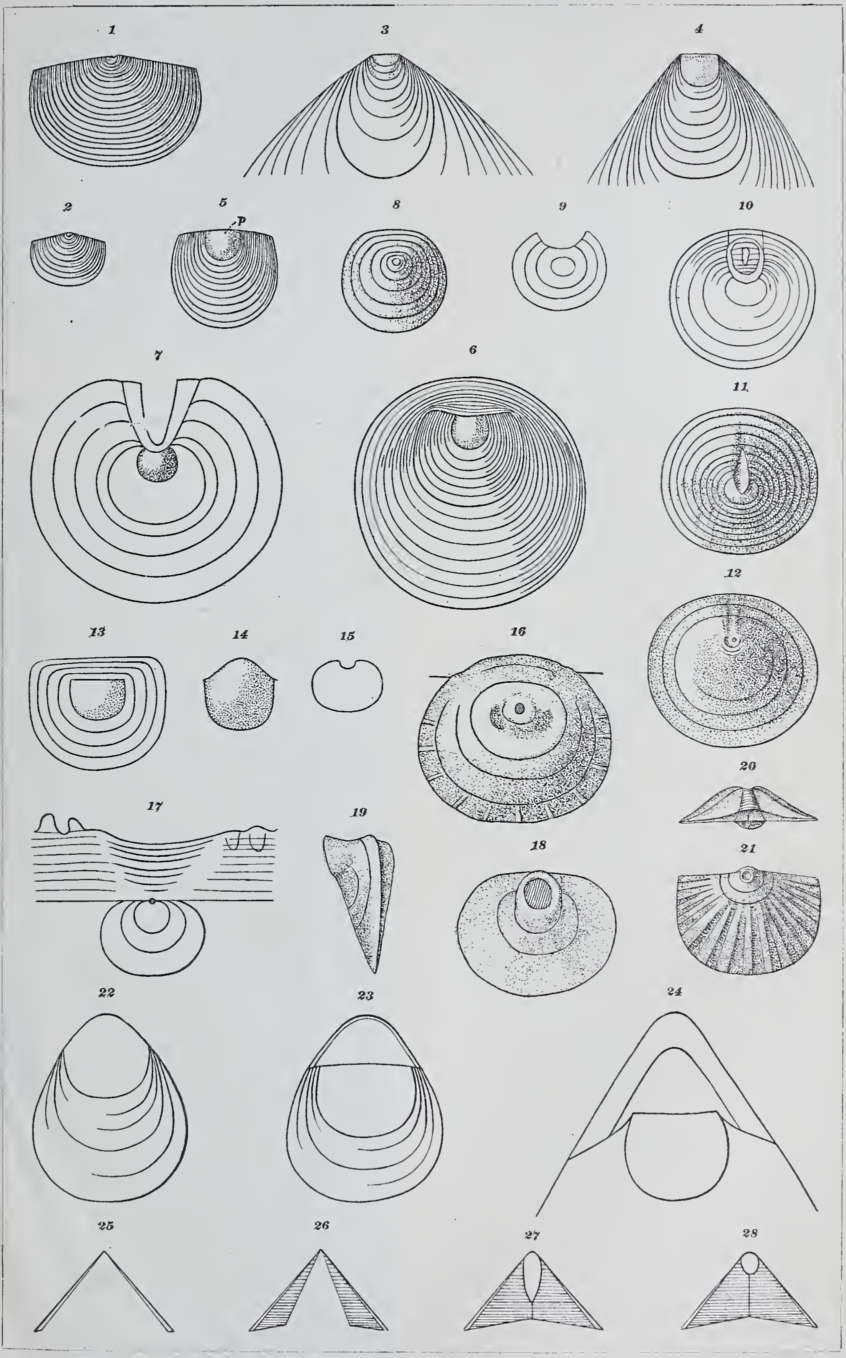
Telotremata.

FIGURE 22.—Ventral view of young *Kraussina* (*Megerlina*) *Lamarckiana*, Davidson; showing protegulum and early nepionic stages. × 80.

FIGURE 23.—Dorsal view of same; showing dorsal protegulum and pedicle opening in ventral valve. × 80. Recent. *Port Jackson, Australia.*

FIGURE 24.—Dorsal view of beaks of young *Terebratulina septentrionalis*, Couthouy; showing dorsal protegulum and pedicle opening in ventral valve. × 80. Recent. *Eastport, Maine.*

FIGURES 25–28.—Diagrammatic representation of ventral areas; showing progressive development of deltidial plates. Figure 25 is without plates, as in ventral area of figure 23. Figure 26 shows two triangular plates, which unite by symphysis in figure 27, making an elongate pedicle opening. In figure 28, pedicle perforation is subcircular and truncates ventral beak. This series corresponds essentially with that shown in *Rhynchotreta cuneata*, Dal., in "Development of Some Silurian Brachiopoda," loc. cit., pl. IV, figs. 16–22.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